NATURAL HYBRIDIZATION BETWEEN SPECIES OF *AMBROSIA* AND *HYMENOCLEA SALSOLA* (COMPOSITAE)

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ABSTRACT

Hybrids between two of the most common shrubs of the Mojave and Sonoran deserts, *Ambrosia dumosa* and *Hymenoclea salsola,* are morphologically distinctive and geographically widespread. At the molecular level, individuals of *A. dumosa* × *H. salsola* can be diagnosed by additivity for distinctive ribosomal DNA markers of the parent species. Individuals of *A. dumosa* × *H. salsola* from the vicinity of Twentynine Palms, California, showed normal meiosis, with 18 pairs of chromosomes at diakinesis and metaphase I, but highly depressed pollen stainability (less than 5%). These results mirror evidence from natural hybrid individuals of *A. ambrosioides* × *H. salsola* from southern Arizona. Crossability and chromosomal similarity between shrubby species of *Ambrosia* and *H. salsola* conforms with phylogenetic evidence from recent morphological and molecular studies that *Hymenoclea* and most species of *Franseria* (now included in *Ambrosia*) are more closely related than previously appreciated. Low pollen stainabilities in the hybrids indicate considerable sterility barriers between the parental taxa, at least via pollen. Nevertheless, putative backcrosses or later-generation hybrids between *A. dumosa* and *H. salsola* in the Twentynine Palms area are known; gene flow between these often-sympatric desert dominants may occur.

Ambrosia dumosa (A. Gray) W. W. Payne and *Hymenoclea salsola* A. Gray are widespread, ecologically important plant species

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MADROÑO, Vol. 43, No. 1, pp. 15–27, 1996

in the Mojave and Sonoran deserts. *Ambrosia dumosa,* a small shrub commonly known as burrobush or burroweed, shares dominance with *Larrea tridentata,* the creosote bush, across ca. 70% of the Mojave Desert (Shreve 1942) and much of the Sonoran Desert (Burk 1977) on well-drained soils at low elevations (up to 1500 m in the Mojave Desert; Vasek and Barbour 1977). *Hymenoclea salsola,* the cheesebush, is a large, dominant shrub in washes up to ca. 1800 m in the Mojave and Sonoran deserts. Across both deserts, *A. dumosa* and *H. salsola* occur in close proximity along washes and in other areas of disturbance.

Ambrosia dumosa and *Hymenoclea salsola* are members of the ragweed subtribe Ambrosiinae (Heliantheae, Compositae), which is diagnosed in part by characteristics that are unusual in the sunflower family: only unisexual flowers, free anthers, and smooth, wind-transported pollen (see Karis and Ryding 1994). *Ambrosia* (including *Franseria*) and *Hymenoclea* are further distinguished from other members of Compositae by a suite of features associated with the unisexual heads. In both genera the staminate heads possess a cup-like involucre of united, uniseriate phyllaries; the pistillate heads are bur-like, with the multiseriate phyllaries coalescent around one or more pistillate florets. Close relationship between *Ambrosia* and *Hymenoclea* was proposed by Peterson and Payne (1973), but both species of *Hymenoclea* have always been treated as generically distinct from other Ambrosiinae.

Ambrosia and *Hymenoclea* differ most noticeably by details of the involucre of pistillate heads. In *Ambrosia* the free tips of pistillate phyllaries are modified into narrow prickles or spines that promote animal dispersal of fruits. In contrast, the phyllary tips of pistillate heads of *Hymenoclea* are membranous, wing-like (non-spinose) structures that presumably promote wind or water dispersal of fruits. *Ambrosia dumosa,* like other species of *Ambrosia* once included in *Franseria,* bears pistillate heads with a distinctly multiseriate involucre of large, spine-tipped phyllaries (Fig. 1). Vegetatively, *A. dumosa* and *H. salsola* are easily distinguished by leaf shape, lobing, and size (Fig. 1). Leaves of *A. dumosa* are ovate to lanceolate, once to thrice pinnatifid or pinnately-lobed, and up to ca. 5 cm long; leaves of *H. salsola* are filiform, generally entire, and ca. 2 to 7 cm long. Leaves and young stems of *A. dumosa* are densely ashy-strigose, giving the plants a greyish blue-green appearance. In contrast, leaves and young stems of *H. salsola* are nearly glabrous, yellow-green, and shiny-glandular.

Herein, we provide evidence of natural hybridization between *A. dumosa* and *H. salsola* in the Mojave Desert, in California, and between *A. ambrosioides* (Cav.) W. W. Payne and *H. salsola* in the Sonoran Desert, in Arizona. The significance of hybridization between shrubby species of *Ambrosia* and *H. salsola* is discussed in

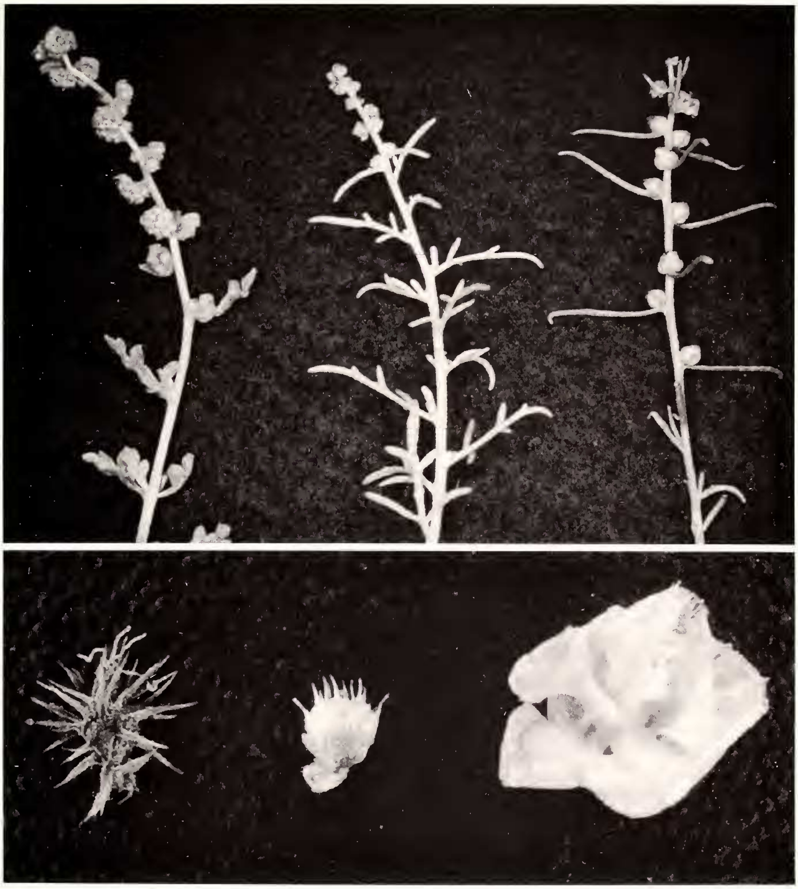

FIG. 1. Flowering branches (top) and pistillate heads (bottom) of *Ambrosia dumosa* (left), *Hymenoclea salsola* (right), and *A. dumosa* × *H. salsola* (center) from near the Kelso Mountains, California.

light of recent investigations of phylogenetic relationships in Ambrosiinae and the possibility of introgression between members of the two genera. We know of no previous documentation in the literature of natural or artificial intergeneric hybridization between members of *Ambrosia* and *Hymenoclea,* apart from unverified reports (e.g., Cronquist, 1994, p. 62).

MATERIALS AND METHODS

Putative hybrids between *Ambrosia dumosa* and *Hymenoclea salsola* were collected near Twentynine Palms, California, in a broad, braided wash (0.16 km north of junction of Sahara Avenue and

TABLE 1. SPECIMENS REFERABLE TO NATURAL HYBRIDS BETWEEN SPECIES OF *AMBROSIA* AND *HYMENOCLEA SALSOLA*.

Ambrosia dumosa × *Hymenoclea salsola*. CALIFORNIA. SAN BERNARDINO COUNTY. Twentynine Palms vicinity: *Baldwin, Kyhos, Martens & Vasek JT780-1, JT780-3, JT780-5, JT780-6, JT780-7* (JEPS). Music Valley, southeast of Twentynine Palms: *Vasek s.n.* (RIV); *Baldwin, Kyhos, Martens, & Vasek JT779-1, JT779-2, JT779-3* (JEPS). Near northwest road entrance to Joshua Tree National Monument, southeast of town of Joshua Tree: *Baldwin, Kyhos, & Martens JT780-11a, JT780-11b* (JEPS). Old Dad Mountain/Kelso Mountains region: *Baldwin, Martens, & M. LaCass 262* (UCSB); *Baldwin OD792-1, OD792-2* (JEPS). Castle Mountains: *D. Charlton 2153 with A. Romsport* (RIV). RIVERSIDE COUNTY. Coachella Valley, east of Fan Hill: *A. Sanders 16,744 with K. Rose* (RIV). NEVADA. NYE COUNTY. Nevada Test Site, Mercury Valley drainage: *R. Hunter s.n. & P. Medica* (ARIZ). MEXICO. BAJA CALIFORNIA. 101.6 km north of San Felipe on Highway 5: *F. Seaman & R. Hartman FS-82(3)* (UC).

Ambrosia ambrosioides × *Hymenoclea salsola*. ARIZONA. PIMA COUNTY. foothills of the Santa Catalina Mountains, Sabino Canyon vicinity: *Baldwin, S. Bainbridge, & R. VanDevender SC788-3, SC788-4* (JEPS); same plants as *T. VanDevender & R. VanDevender 90-47* (ARIZ, ASU), *91-524* (ARIZ), *91-525* (ARIZ). MARICOPA COUNTY. South Mountains: *M. Butterwick and T. Daniel 8874* (CAS).

Morning Drive; *Baldwin, Kyhos, Martens & Vasek JT780-1, JT780-3, JT780-5, JT780-6, JT780-7* (JEPS)). Five plants were uprooted and greenhouse-propagated for morphological, cytological, pollen, and molecular studies at the University of Arizona, Tucson, and (later) at Duke University. Material of two putative hybrids between *A. ambrosioides* and *H. salsola* was collected at 0.6 km and 1.0 km above the Sabino Canyon Recreation Area Visitor's Center along the road to Sabino Canyon in the foothills of the Santa Catalina Mountains, north of Tucson, Arizona [*Baldwin, S. Bainbridge, & R. VanDevender SC788-3, SC788-4* (JEPS); the same plants as *T. VanDevender & R. VanDevender 90-47* (ARIZ, ASU), *91-524* (ARIZ), *91-525* (ARIZ)]. Other putative hybrids between *A. dumosa* and *H. salsola* and between *A. ambrosioides* and *H. salsola* examined morphologically are listed in Table 1.

Morphological characters that showed marked variation among the putative hybrids and suspected parental species were measured or described from pressed, dried, field specimens. Individuals grown in cultivation under uniform conditions were examined for any variation in phenotypic characteristics.

Buds of staminate heads from the putative hybrids and parental species were fixed in modified Carnoy's solution (6 parts chloroform : 3 parts absolute ethanol : 1 part glacial acetic acid) for five days at room temperature and stored at −20°C prior to chromosomal analysis. Chromosomes were examined at diakinesis and meiotic metaphase I in squashed microsporocytes stained with acetocarmine mixed with Hoyer's solution. Pollen of putative hybrids and parents was treated with cotton blue in lactophenol and examined for stainability.

Total DNAs were extracted from two grams of fresh leaf material from one individual each of *A. dumosa* [*Baldwin, Kyhos, Martens, & Vasek JT779-4* (JEPS)], *H. salsola* [*Baldwin SC788-1* (JEPS)], and the five greenhouse-propagated, putative hybrids between the two species using a modified CTAB method (Doyle and Doyle 1987), with one isopropanol precipitation, two ethanol precipitations, and purification of DNAs on cesium chloride gradients. Single-stranded DNAs of the internal transcribed spacer (ITS) region of 18-26S nuclear ribosomal DNA in *A. dumosa* and *H. salsola* were amplified by asymmetric polymerase chain reactions (PCR) using a 20:1 ratio of primers "ITS4" and "ITS5", following the procedures of Baldwin (1992). DNA sequences of ITS 1 of both species were obtained by Sanger sequencing of the purified single-stranded PCR products, using the "ITS5" primer as the sequencing primer (see Baldwin 1992). Restriction maps of the two DNA sequences were constructed using DNA Strider (Marck and CEA 1989) and examined for diagnostic differences. Double-stranded DNAs of the ITS region of *A. dumosa, H. salsola,* and the five putative hybrids were amplified using symmetric PCRs using an equimolar ratio of primers "ITS4" and "ITS5" (see Baldwin 1992). Purified PCR products were digested to completion with *Bsm*A I and *Spe* I, using the recommended reaction conditions (New England Biolabs). Digested PCR products were electrophoresed on 4% agarose gels (3% NuSieve, 1% LE; FMC) with a 123 base-pair (bp) ladder (Gibco BRL) of molecular weight markers, stained with ethidium bromide, and examined on an ultraviolet light transilluminator.

Results

Putative hybrids between species of *Ambrosia* and *Hymenoclea salsola* show intermediacy or combinations of character-states of the suspected parental species in characters associated with foliage coloration, leaf shape, and numbers and shapes of phyllaries in pistillate heads. Morphological characteristics of putative hybrids between *A. dumosa* and *H. salsola* were retained under greenhouse conditions, as was strong morphological uniformity among the five individuals. Foliage of suspected hybrids between *A. dumosa* and *H. salsola* is distinctly greyish olive-green, rather than yellow-green or greyish blue-green, which allows the plants to be identified at a distance. Leaves of putative hybrids of the combination *A. dumosa* × *H. salsola* are ovate in outline, as in *A. dumosa,* with filiform or narrowly linear leaf segments, like *H. salsola* (Fig. 1). Phyllaries of pistillate heads combine characteristics of both suspected parental species (Fig. 1): scarious margins (like *H. salsola*), length ca. twice the width (intermediate), and presence of a rigid midrib and apical spine (like *A. dumosa*). In all of the above characteristics, the putative hybrids between *A. dumosa* and *H. salsola* conform to those in the description, illustration, and isotype [*F. Seaman & R. Hartman FS-82* (UC!)] of *H. platyspina* Seaman from northern Baja California (Seaman 1975). Putative hybrids between *A. ambrosioides* and *H. salsola* show parallel patterns of similarity with the suspected parental species, with intermediacy in foliage characteristics and numbers and dimensions of phyllaries in pistillate heads (Figs. 2, 3). As in the suspected parent *A. ambrosioides,* the putative hybrids have leaves that are narrowly deltate in outline and phyllaries of pistillate heads with strong midribs, apical spines, and (sparse) glandular pubescence. As in *H. salsola,* the putative hybrids have leaves with narrow segments and phyllaries of pistillate heads with scarious margins.

Analysis of chromosomes in putative hybrids of both combinations revealed no evidence of reduced pairing or genomic structural heterozygosity. Eighteen pairs of chromosomes were seen in all of 111 diagnostic microsporocytes (38 in one plant, 73 in the other) examined in two putative hybrids of the combination *Ambrosia dumosa* × *Hymenoclea salsola* (Twentynine Palms vicinity) and in all of 20 diagnostic microsporocytes examined from one putative hybrid of the combination *A. ambrosioides* × *H. salsola* (Sabino Canyon vicinity). Chromosomal analysis of *A. dumosa* from near Twentynine Palms [*Baldwin, Kyhos, Martens, & Vasek JT780-9* (JEPS)] revealed that the plants in proximity to the putative hybrids were diploids, with n = 18, rather than tetraploids or hexaploids, which are also known to occur widely in the Mojave Desert (Raven et al. 1968).

Pollen stainability, a direct indicator of pollen viability, in each of two plants of the putative hybrid combination *Ambrosia dumosa* × *Hymenoclea salsola* from near Twentynine Palms and in both putative hybrids of *A. ambrosioides* × *H. salsola* from near Sabino Canyon was less than 5%. Pollen samples from herbarium specimens of putative hybrids of the combination *A. dumosa* × *H. salsola* from nw of the Kelso Mountains, south of Baker, California [*Baldwin, Martens, & M. LaCass 262* (JEPS)], and of the putative hybrid combination *A. ambrosioides* × *H. salsola* from the South Mountains near Phoenix, Arizona [*M. Butterwick and T. Daniel 8874* (CAS)], were also less than 5% stainable. In contrast, pollen stainabilities of individuals of all suspected parental species from the vicinity of putative hybrids were greater than 65%.

Restriction digests of PCR products of the ITS region from individuals of *Ambrosia dumosa, Hymenoclea salsola,* and five putative hybrids from near Twentynine Palms yielded diagnostic markers for *A. dumosa* and *H. salsola,* all of which were present in the

FIG. 2. *Hymenoclea salsola* (top), *Ambrosia ambrosioides* (bottom), and *A. ambrosioides* × *H. salsola* (center) from near Sabino Canyon, Santa Catalina Mountains, Arizona.

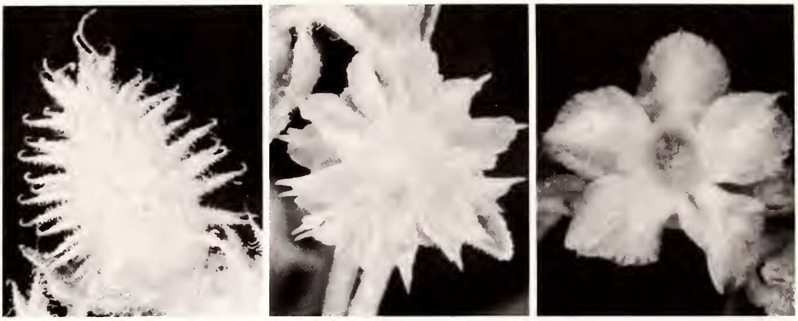

FIG. 3. Pistillate heads of *Ambrosia ambrosioides* (left), *Hymenoclea salsola* (right), and *A. ambrosioides* × *H. salsola* (center).

five putative *A. dumosa* × *H. salsola* plants. With *Spe* I, the ITS products of *A. dumosa* were digested into two fragments of ca. 150 bp and ca. 600 bp; the ITS products of *H. salsola* were undigested and ca. 750 bp (Fig. 4). ITS products of the five putative hybrids digested with *Spe* I showed additivity for the two bands observed in the digest of ITS products of *A. dumosa* and the intact product of *H. salsola* (Fig. 4). With *Bsm*A I, the digested ITS products of *A. dumosa* included two fragments of ca. 200 bp and ca. 350 bp; the digests of ITS products of *H. salsola* lacked similar fragments and included, instead, a fragment of ca. 550 bp, absent from *A. dumosa.* Digests of the ITS products of the five putative hybrids from Twentynine Palms with *Bsm*A I showed additivity of the ca. 200 bp and ca. 350 bp fragments seen in the *A. dumosa* lane and the ca. 550 bp fragment observed in the *H. salsola* lane.

DISCUSSION

Comparisons of morphology, pollen stainability, and ITS sequences among putative hybrid individuals of the combination *Ambrosia dumosa* × *Hymenoclea salsola* and the suspected parent species confirm natural hybridization between the two species in the vicinity of Twentynine Palms. Uniformity of morphological characteristics among the five hybrid individuals grown under similar greenhouse conditions strongly suggests that the plants are of the F_1 generation. Similarities in morphology and pollen stainability between the hybrids near Twentynine Palms and collections from the Kelso Mountains vicinity identify the Kelso Mountains plants as additional examples of natural hybrids between *A. dumosa* and *H. salsola.* Other plants referable to the combination *A. dumosa* × *H. salsola* include *H. platyspina* Seaman from the Sonoran Desert of Baja California (Seaman 1975), and collections from California and

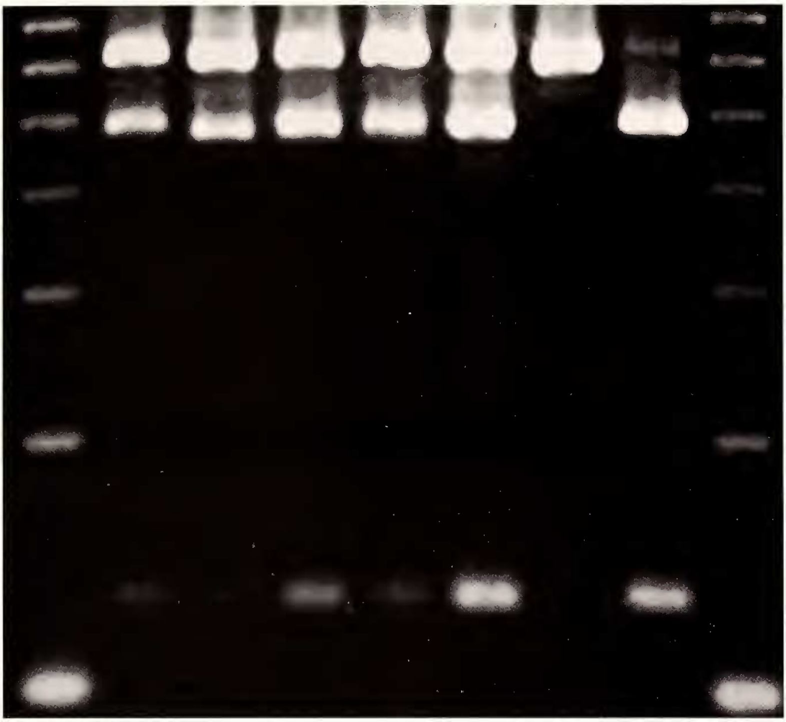

FIG. 4. Electrophoresed *Spe* I restriction fragments of the internal transcribed spacer region of nuclear ribosomal DNA from *Ambrosia dumosa, Hymenoclea salsola,* and five interspecific hybrids collected near Twentynine Palms, California. From left to right, a 123 bp ladder of molecular weight markers (lanes 1, 9), *A. dumosa* × *H. salsola* plants (lanes 2 thru 6), *H. salsola* (lane 7), and *A. dumosa* (lane 8). Note additivity for the markers of both parental species in the hybrids.

Nevada listed in Table 1. The parentage of *A. sandersonii* S. L. Welsh [*H. sandersonii* (S. L. Welsh) N. H. Holmgren], from Utah, is still uncertain and may have involved *A. eriocentra* (A. Gray) W. W. Payne and *H. salsola,* as contemplated by Welsh (1993). Vegetative and reproductive morphology of *A. sandersonii* and low pollen stainability (2.6%) in the isotype at CAS (*S. Sanderson 93-02*) indicate hybridity between a shrubby franseria and *H. salsola.*

Morphological characteristics and low pollen stainabilities of the two putative hybrids between *Ambrosia ambrosioides* and *Hymenoclea salsola* from Sabino Canyon verify natural hybridization between the two species. Similar morphology and pollen stainability of a plant collected from the South Mountains near Phoenix, Arizona (Table 1), indicate that that individual is referable to the same hybrid combination.

Lack of previous documentation of hybridization between members of *Ambrosia* and *Hymenoclea salsola* is surprising; the taxa cooccur widely in areas with varying levels of natural and human-caused disturbance. Natural hybridization between *A. dumosa* and *H. salsola,* in particular, appears to be a widespread phenomenon. Herbarium specimens (Table 1), personal communications (e.g., with B. Turner, D. Keil, B. Prigge, V. Yoder), and unverified reports (Cronquist 1994, p. 62) demonstrate that other botanists have suspected hybridization between *A. dumosa* and *H. salsola.* In recognition of the recurrent formation of natural hybrids between the two species across a broad geographic range, we here adopt the name *H.* ×*platyspina* Seaman based on *H. platyspina* Seaman pro sp. (Seaman, F. 1995. Madroño 23:111) for plants of the combination *A. dumosa* × *H. salsola.*

Systematic implications of hybrids. Close genetic similarity of *Ambrosia dumosa* and *A. ambrosioides* to *Hymenoclea salsola* is evident from normal pairing of chromosomes in interspecific hybrids. Low pollen fertilities of the intergeneric hybrids indicate that genetic differences between the parental species are nevertheless sufficient to impact fertility. Similarly, low pollen fertilities have been observed in other hybrid combinations with normal chromosomal pairing at meiosis, as in *Wedelia biflora* (L.) DC. × species of *Lipochaeta* sect. *Aphanopappus* (Rabakonandrianina and Carr 1981), and have been attributed to cryptic structural differences between the parental genomes (Stebbins 1950, 1971) or finer-scale genetic problems. Irrespective of levels of hybrid fertility, natural hybridization and normal pairing of chromosomes between members of different plant genera have rarely been reported, as might be expected if placement of species in different genera implies more ancient divergence from a common ancestor than the time of divergence of congeneric taxa (an assumption that is certainly not universally true). Hybridization between species of *Ambrosia* and *Hymenoclea* may reflect inadequacy of the long-standing generic classification of Ambrosiinae to express evolutionary relationships within the subtribe.

Results from recent phylogenetic investigations of Ambrosiinae based on morphological and chloroplast DNA (cpDNA) restriction site variation demonstrate that relationships between species of *Ambrosia* and *Hymenoclea* have been misunderstood. Wagner parsimony analysis of cpDNA restriction site data from members of *Ambrosia* sensu lato (including *Franseria*) and *Hymenoclea* by Miao et al. (1995) resolved a strongly supported (95% bootstrap) lineage comprised of *Hymenoclea salsola* and five species of franseria (including all shrubby taxa sampled), to the exclusion of *H. monogyra,* two species of franseria, and all species sampled of *Ambrosia* sensu stricto. *Hymenoclea monogyra* was resolved as sister to the *H. salsola/Franseria* lineage, exclusive of *Ambrosia* sensu stricto and two species of franseria. Based on their cpDNA results, Miao et al. (1995) proposed that *Hymenoclea* be submerged taxonomically within *Ambrosia.* Results from a phylogenetic analysis of Ambrosiinae based on morphological data (Karis 1995) corroborate nonmonophyly of *Ambrosia* sensu Payne (1964), with *Hymenoclea* resolved as sister to a lineage of two shrubby species of franseria, *A. eriocentra* and *A. ilicifolia,* to the exclusion of herbaceous species of *Ambrosia* sensu stricto (and *Xanthium*). The surprisingly close relationship of shrubby franseria species and *H. salsola* revealed by both phylogenetic investigations accords well with normal pairing of chromosomes in the natural hybrids reported here.

Karis's (1995) phylogenetic study of Ambrosiinae is also pertinent to the issue of hybridization between species of *Ambrosia* and *Hymenoclea salsola* because of inclusion of *H.* ×*platyspina,* i.e., the hybrid between *A. dumosa* and *H. salsola,* as a terminal taxon in his analysis. In the cladogram presented by Karis, *H.* ×*platyspina* is sister to a lineage consisting of *H. monogyra* and *H. salsola.* In turn, the three species of *Hymenoclea* are sister to shrubby species of franseria in Karis's tree. Absence of any derived morphological characteristics on the *H.* ×*platyspina* phylogeny branch and the placement of *H.* ×*platyspina* as sister to the rest of *Hymenoclea* in the cladogram support Karis's conclusion that the "species" is ". . . provided with characters that are 'transitional' between the two genera" (*Ambrosia* and *Hymenoclea*). The data presented here indicate that the "transitional" morphology of *H.* ×*platyspina* is not attributable to retention of characteristics of the most recent common ancestor of *Hymenoclea* species, but to origin of the plants via hybridization between *A. dumosa* and *H. salsola.*

Ecological implications of hybridization. The possibility of gene flow between species of *Ambrosia* and *Hymenoclea* is intriguing from an ecological perspective, especially with respect to the widespread species *A. dumosa* and *H. salsola.* Co-occurrence of *A. dumosa* and *H. salsola* in complex mosaics of natural disturbance over much of the Mojave and Sonoran deserts may offer diverse ecological opportunities for hybrids and backcrosses involving the two species. The tremendous success of *A. dumosa* and *H. salsola* across broad areas and environmental gradients may prove to be attributable in part to occasional gene flow between the species.

Low pollen stainability in the *Ambrosia/Hymenoclea* hybrids indicates limited potential for backcrossing or later-generation hybridization between species of the two genera. Ovulate fertility has not been assessed in the hybrids and could be considerably higher than pollen fertility, as seen in many hybrid combinations in plants (cf.

Rieseberg, 1995). If microhabitats wherein hybrids are better fit than parents exist in proximity to the parental species, then backcrossing and introgression might proceed even in the face of high levels of hybrid sterility in pollen and ovules, especially if the plants involved are long-lived perennials with recurrent opportunities for reproduction, as in the study species.

At the Twentynine Palms site, putative backcross plants were observed with morphological characteristics that appeared overall more like those of *A. dumosa* than those of the *A. dumosa/H. salsola* hybrid individuals. Follow-up studies that examine hybrid fruit set, hybrid seed viability, and characteristics of any viable progeny of the hybrids described in this investigation might prove enlightening about the natural potential for introgression between the species. Detailed research on the genetic constitution of individuals in areas of hybridization, such as the Twentynine Palms site, would be especially valuable to test rigorously the occurrence of gene flow between these desert plants.

Acknowledgments

We thank Becky VanDevender and Tom VanDevender for assistance with obtaining material of the *Ambrosia ambrosoides/Hymenoclea salsola* hybrids from Sabino Canyon (discovered by Joan Tedford of Sabino Canyon Recreation Center), Tom Daniel for material of *A. ambrosioides/H. salsola* hybrids from the South Mountains, Jochen Schenk for helpful discussions, John Strother for reviewing the manuscript, Bill Whitehead for assistance in preparing the figures, and the Southern California Botanists for inviting the first author to their 1995 symposium on Botany of the Eastern Mojave Desert, where the results reported here were first presented.

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(Received 7 Apr 1995; accepted 17 May 1995)